Maturation is basipetal in the inflorescence as a whole. Upper first and second order branches produce the first flowers (Tomlinson & Moore, 1968, *Fig. 40*).

The further expansion of specific lateral branches is not uniform but can be related to the order of the branch. Third order branches mature acropetally, but development of fourth order branches is irregular. Mature flowers are produced on some fourth order axes when others are still in early stages of development as illustrated by FIGS. 1–3. In early stages of growth, some fourth order branches are equal in size to the main branch (third order axis) on which they are borne (FIG. 1). The result is a digitate configuration, which may be useful in interpreting digitate branching in mature inflorescences elsewhere in palms. In a later stage (FIG. 2) some of the fourth order branches have matured while others are still undeveloped.

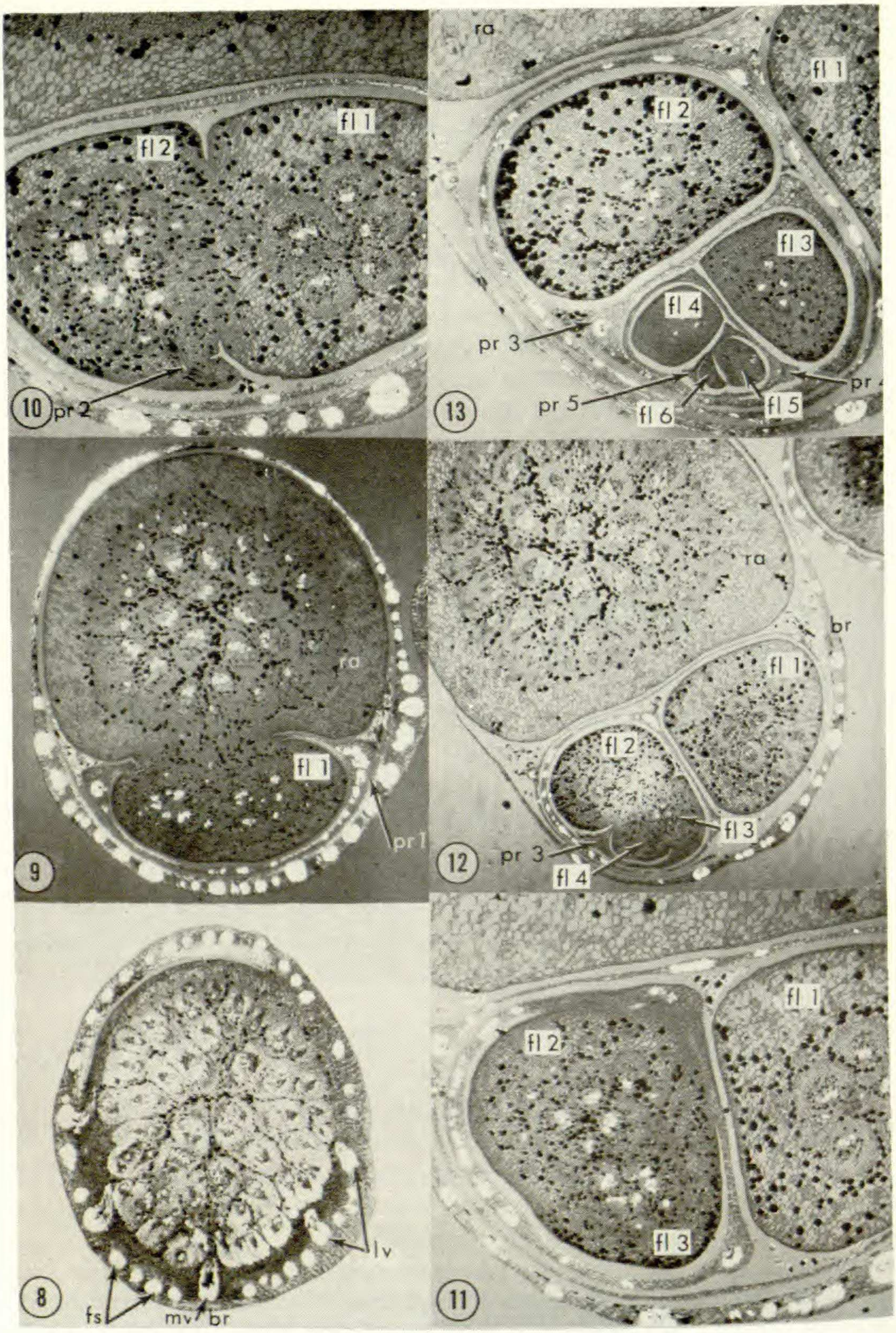
Flowers may mature irregularly on a specific rachilla. Those in cincinni at the middle of the rachilla often develop before those in cincinni nearer the base or the apex (FIG. 3), but in general the order of development is acropetal. Within each cincinnus there is still another acropetal series in the maturation of individual flowers (FIG. 4).

Anatomy. The vascular system in rachillae is composed of a central or subcentral group of about 10 (8–12) large vascular bundles with a number (ca. 13) of intermediate and smaller bundles peripheral to them (FIGS. 8, 9, 12). The peripheral bundles represent strands which supply cincinni, and they vary in number and position depending on the proximity of the level examined to a cincinnus. Each large bundle has 1 to 4 large vessels (FIG. 12) and a complete fibrous sheath which is approximately 5 to 7 cells wide over the xylem. Most commonly there are two large vessels per bundle, but bundles about to branch have three large vessels and small branch bundles only one. The narrow cortex is of small unspecialized parenchyma 6 to 8 cells in width, and the epidermis is of smaller isodiametric cells.

BRACTS

Morphology. Two types of bracts may be present on rachillae. On first, second, and third order branches there is usually an irregularly bicarinate prophyll which is inserted basally in an adaxial position. This bract is commonly empty on first and second order branches but on third order branches it subtends the first lateral branch.

Flower clusters are subtended not by prophylls but by irregularly funnel-shaped bracts with attenuate dorsal tips. Similar but larger bracts borne on one axis and subtending branches of the next order occur throughout the inflorescence and may be arranged in a reduction series from a foliage leaf (Tomlinson & Moore, 1968). Bracts subtending cincinni are the smallest of the series and are all equal in size and shape at maturity. On fully expanded rachillae, each bract is about 3 mm. long, the sheathing part extending for ca. 2 mm. of this.



FIGS. 8–13. Successive transections of a cincinnus, taken in polarized light. FIG. 8, transection of rachilla and bract subtending a cincinnus, × 18; FIG. 9, transection of rachilla and axis of the first flower, × 18; FIG. 10, transection at level of origin of lower trace to prophyll on second flower, × 36; FIG. 11, transection at level of origin of upper trace to prophyll on second flower, × 36; FIG. 12, transection of rachilla and stalks of first, second, third, and fourth

Anatomy. Each bract subtending a cincinnus is supplied by five vascular bundles and by a large number of fibrous strands (FIGS. 6, 8, 9). The vascular bundles, which may be designated as a midvein and two pairs of lateral bundles, originate as small branches of peripheral stelar strands. The continuing vertical bundles (Zimmermann & Tomlinson, 1965) from which the midvein and first pair of lateral bundles originate usually enter the stalk of the first flower. Vertical bundles providing the second pair of laterals, however, continue in the rachilla. Lateral vascular bundles branch and anastomose distally in the bract (FIG. 6). The numerous fibrous strands (FIGS. 6, 8) are wide tangentially and also branch and anastomose distally. They are tapered somewhat proximally but are not connected to the vascular cylinder of the rachilla.

FLOWERING UNITS

Morphology. With the initiation of the first flower, the growth pattern of the inflorescence shifts from monopodial to a sympodial elaboration of clusters, each consisting of five or six successively younger flowers (FIG. 4). The bract on the rachilla subtends the first flower. The stalk of this flower in turn bears an adaxially situated bracteole which is completely sheathing and has two subequal adaxial tips, thus differing from the bract subtending the first flower and definable as a prophyll. The prophyll subtends the second flower of the cluster. The stalk of the second flower bears a similar bracteole which subtends the third flower. This pattern is repeated up to five or six times in *Nannorrhops* (FIGS. 8–13). Each floral primordium is initiated on the opposite side of the appropriate floral stalk and at an angle of approximately 75°. Although five or six buds are present in the cluster, only three flowers usually mature. Because flowers are successively younger and pedicels elongate successively during maturation, the two-rowed condition of a cincinnus, though structurally present, is not readily evident macroscopically. Left-handed and right-handed cincinni occur, depending on whether the second flower is initiated on the left or right side of the first floral axis. A specific rachilla usually bears predominantly left- or right-handed clusters — e.g. on a right-handed rachilla only one or two basal and one or two median cincinni are left-handed.

Anatomy. Bundles which supply the first flower of a cincinnus originate as branches of major axial bundles in the rachilla. The first such branch originates at about the level of insertion of the second cincinnus

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flowers, × 18; FIG. 13, transection through all flowers of a cincinnus, × 36. DETAILS: br, bract subtending first flower of a cincinnus; fl 1 to fl 6, successive flowers of a cincinnus; fs, fibrous bundles of bract; mv br, midvein of bract; lv, lateral vascular bundles of bract subtending first flower; pr 1, prophyll borne on axis of the first flower; pr 2, prophyll of second flower, arrow points to lower trace; pr 3, prophyll of third flower; pr 4 and pr 5, prophylls of fourth and fifth flowers respectively; ra, rachilla.

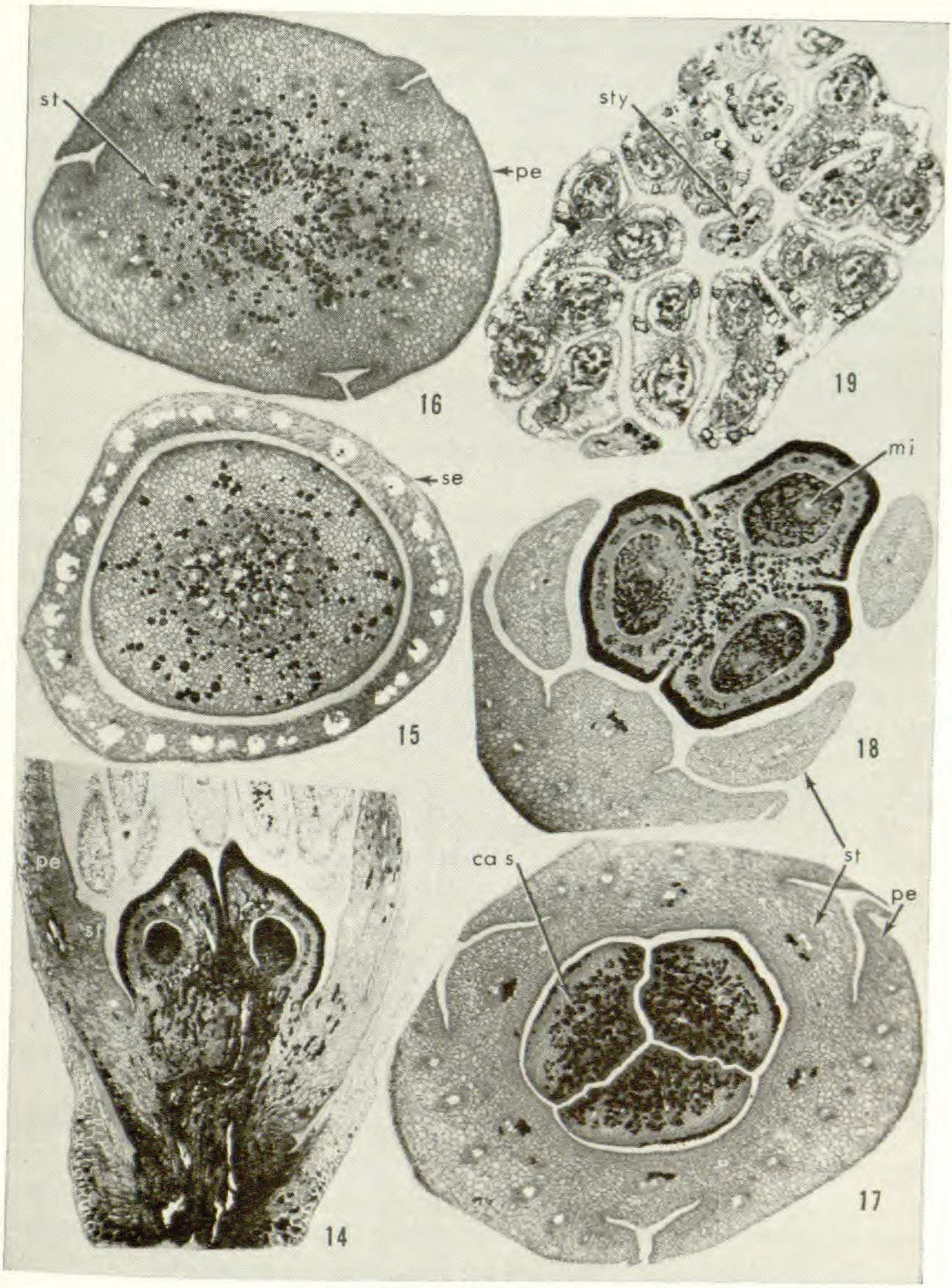
below. About three more branches are derived from axial bundles at higher levels, and further branching of these provides the complete supply to the first flower. At the level of origin of the midvein of the subtending bract, this supply consists of a group of about 16 bundles. The exact number of bundles is somewhat subjective unless the level is carefully indicated, since bundles are frequently small, especially near their origin, and fibrous bundle sheaths are often confluent for some distance.

Anatomically as well as morphologically prophylls are different from other bracts in the inflorescence. The main vascular complement of each prophyll is two vascular bundles, one supplying each tip (FIGS. 9, 11, 13). These traces are derived as small branches of marginal stelar bundles of the floral stalk. The bracteole is obliquely inserted and irregularly bicarinate, one tip being slightly longer than the other. The trace to the longer tip originates at a slightly lower level than that to the shorter (FIG. 11), and is a somewhat larger bundle which often branches distally. Unconnected fibrous strands are also present in the prophyll (FIG. 11) and occasionally a third vascular bundle (FIG. 11) is seen.

Above the origin of the traces to the first bracteole, the stelar bundles of the first flower provide the vascular supply to the second floral stalk (FIGS. 8, 9, 20). Two of the ensuing bundles produce small branches, each supplying one tip of the second prophyll (FIGS. 10, 11), and the pattern is repeated until up to five or six floral primordia are formed (FIGS. 8–13, 20). Thus anatomically each flower, its axis, and bracteole are identical to the others making up the cincinnus. Transections of the floral axes of the first, second, third, and fourth flowers may be compared in FIGURES 10, 12, and 13 and their similarity noted. The pattern of origin of the vascular supply to each floral stalk is also similar as can be seen in FIGURE 20 which is a camera lucida drawing of the major bundles in a cleared cincinnus.

THE FLOWER AT ANTHESIS

Morphology. Among the palms, approximately 165 genera are monoecious, about 39 are dioecious, and some 34 genera bear perfect flowers. *Nannorrhops* belongs among the last, having perfect flowers with three sepals, three petals, six stamens, and a tricarpellate gynoecium. Open flowers (FIG. 5) are approximately 6 mm. long. The sepals are 3 mm. long and are connate for two-thirds this length forming a sheath, above which the membranaceous tips are free. Petals are ca. 5 mm. long, ovate, somewhat fleshy, shortly imbricate near the base and then valvate. Stamen-filaments are wide and fleshy basally (FIGS. 5, 18), but taper to the attachment of the versatile anthers which are subequal, basally divergent, and laterally dehiscent. The three carpels are free in young stages, but in mature flowers are connate by ventral faces through the ovarian and stylar regions. Thus at anthesis the gynoecium is syncarpous with definite external grooves showing the limits of each carpel. Each carpel has a distinct stalk, an ovoid fertile part, and a long attenuate style through which



FIGS. 14–19. Sections of mature flowers, taken in polarized light. FIG. 14, tangential longisection with two carpels, × 20; FIG. 15, transection through sepal tube and floral axis at level of origin of petal traces, × 36; FIG. 16, transection through base of flower above FIG. 15, × 36; FIG. 17, transection at higher level where carpel stipes are distinct, × 36; FIG. 18, transection of ovarian part of gynoecium, carpels connate, × 36; FIG. 19, transection of anthers and style, × 36. DETAILS: *ca s*, *carpel stipe*; *mi*, *micropyle*; pe, petal; se, sepal tube; st, stamen trace; sty, style.

a locular canal extends to open distally. There is no connection (compitum, Carr & Carr, 1960) between locular canals of adjacent carpels. No definite stigmas are present. Papillose stigmatoid tissue is apparently present at anthesis around the stylar opening but is not developed until the flower opens. An anatropous ovule is attached ventrally and basally in each locule and is turned so that the micropyle is lateral rather than dorsal in respect to the funiculus.

At anthesis about one-third the length of the flower consists of a tapered solid basal part (FIG. 5) sheathed by the sepal tube and representing the region of insertion of petals, stamens, and carpels. A very short petal-stamen tube surrounds the free carpel stalks (FIGS. 14, 17) but since all organs are free just *below* the ovary in the mature flower, the short petal-stamen tube does not seem to justify the term "perigynous."

Anatomy. Floral anatomy in *Nannorrhops ritchiana* has been described by Morrow (1965) and Gupta (1960). The present study confirms most of the observations of these authors and provides further details of carpel anatomy, organogeny, and histogenesis. The general outlines of the floral vascular system can be seen in FIG. 7 which is a cleared preparation of the central part of a flower. Just below sepal insertion, bundles present in the floral stalk enlarge, extend peripherally, and branch forming a group of bundles which provide traces to the floral organs. Further details of this pattern are presented in a radial plot of one of the large axial bundles (FIG. 23). The pattern is irregular in that traces to floral organs are branches originating near the insertion of the organ *or* at a lower level.

Gupta (1960) reports two rings of bundles in the floral pedicels: an outer of 11 or 12 and an inner of three larger ones. Morrow (1965) states that 9 (8 to 10) strands enter the base of the flower. Three central strands do mature first in floral stalks and are often larger (FIGS. 12, 13). In mature pedicels both large and small bundles are present with a gradual transition in size. The number of bundles is somewhat subjective because of the difficulty of getting exactly comparable levels. In the material I studied, 10 to 15 bundles were present, five or six showing birefringent xylem (FIGS. 10, 12, 13).

Just below sepal insertion, larger bundles of the stalk extend toward the periphery, become larger, and branch (FIG. 7). Smaller bundles may fuse with larger ones or also branch. The floral stele, at the level of sepal insertion, consists, therefore, of about 20 to 25 medium to small bundles, arranged in a thick ring, the larger bundles toward the center. Fifteen (14 to 18) small sepal traces originate as branches of peripheral bundles of this stele. Sepal traces near their origin consist of a few sieve elements and two to four xylem elements and are very easily overlooked; but slightly higher in the sepal-tube, fibrous caps are present on these bundles and unconnected fibrous bundles are present between vascular strands. Thus a ring of approximately 28 bundles is present in a transection of the sepal-tube (FIG. 15). Five vascular bundles with four to six interspersed

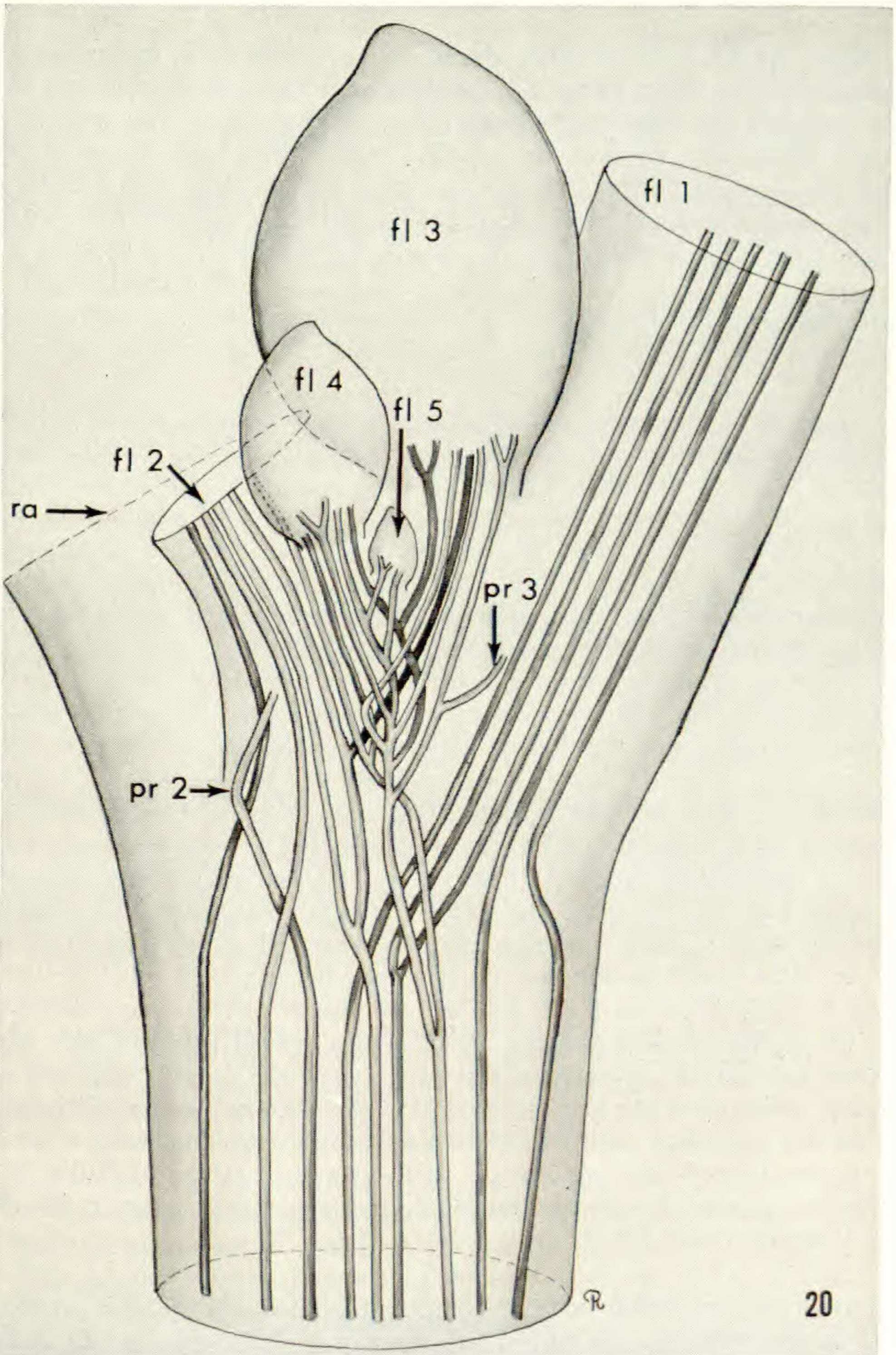


FIG. 20. Wash drawing of a cleared cincinnus, done with Wild M5 stereomicroscope and drawing attachment, to show major vascular supply to flowers. First two flowers, fl 1 and fl 2, abscissed; younger flowers, fl 3 to fl 5, in bud; pr 2, one trace to the prophyll borne on the second flower; pr 3, one trace to the prophyll of the third flower; ra, rachilla.

fibrous strands represent the supply to each sepal, a midstrand and two laterals reaching the tip.

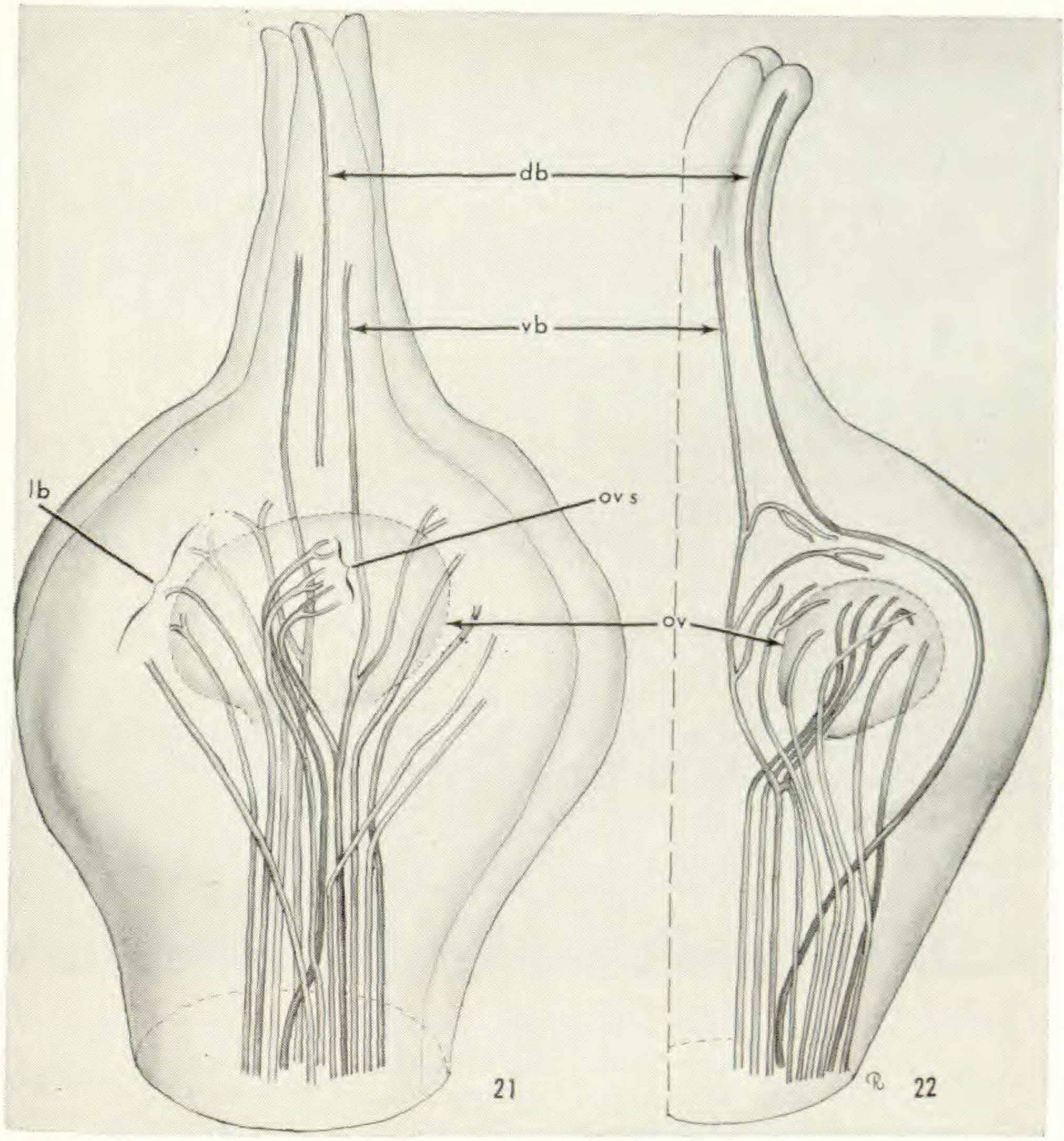
There are six to nine traces, situated in a median row, in the base of each petal (FIG. 16). These may be stelar bundles extending directly into the petal or they may be branches of a stelar bundle. The number of traces varies slightly. Morrow (1965) reports three and Gupta (1960) five from receptacular strands and one from a perianth-stamen bundle. A single median procambial strand develops first in each petal followed by three strands at a later stage in ontogeny. The two laterals from this group of three divide very near the central stele and with the midvein and one or more small traces from the receptacle form the seven major strands (FIGS. 16, 17). These often produce parallel branches at higher levels.

Traces to stamens arise in two whorls in the same manner as petal supplies by the branching or direct conversion of a vertical bundle into a stamen trace. Antipetalous traces may arise as a branch of the same vertical bundle which formed the median petal trace, or as a branch or conversion of an adjacent bundle. Stamen traces are large bundles which divide in the base of the filament (FIGS. 17, 18) into two traces which are oriented xylem to xylem in the filament with the phloems lateral in position, but which reunite in the distal part of the filament.

In the receptacle below the gynoecium, about ten large vertical bundles (bright spots, FIG. 16) are arranged in a central ring with smaller strands external to them. Slightly higher, all stelar bundles are divided into three groups, one of which supplies each carpel stalk. Some 14 bundles are present in a close group in the lower part of each stalk. One of the larger bundles becomes the dorsal bundle of each carpel and the others form the lateral and ventral bundles. There are usually four major pairs of lateral bundles and two ventrals (FIG. 21). The latter may be distinguished by position and by their extension with the dorsal bundle higher into the style. Other small bundles are aligned along the ventral face of the locule and at anthesis extend about one-half the length of the ovary. Branches of the ventral bundles and the dorsal bundle extend into the style while lateral bundles and branches of the ventrals and the dorsal vascularize the ovary wall around the locule (FIGS. 21, 22). Two or three small bundles from the carpellary stele remain in median positions and, with a branch from one ventral bundle, form the ovular supply. In the funiculus these bundles are nearly confluent but divide into separate bundles in the chalazal region (FIGS. 21, 22).

ORGANOGENY

The value of broadening surveys of floral anatomy to include organogeny and histogenesis has been emphasized recently (Tepfer, 1953; Esau, 1965; Kaplan, 1968). Gupta (1960) includes a brief description of organogeny in *Nannorrhops*, but floral histogenesis has not previously been done for a palm. The difficulty of obtaining suitable stages for such



FIGS. 21, 22. Wash drawings of cleared gynoecia, prepared as for FIG. 20. FIG. 21, entire gynoecium showing only bundles of the nearest carpel in dorsal view, dorsal bundle (db) not completed for clarity; FIG. 22, lateral view of part of a cleared gynoecium showing traces of one carpel, one ventral and the corresponding lateral bundles omitted for clarity. DETAILS: db, dorsal bundle; lb, lateral bundles; ov, ovule; ov s, ovular supply.

studies in most palms is obvious. In *Nannorrhops*, however, particularly fortunate sequences in maturation of both inflorescence branches and flowers occur. FIGURE 4 shows a cincinnus made up of five successively younger flowers. Cincinni mature acropetally on their respective branches (FIG. 3). Further, there is a lag in maturation of basal branches, so that rachillae with young stages and others with flowers at anthesis may be present on the same branch. Thus, because of a developmental pattern that results in mature flowers over a long period of time, necessary material for ontogenetic investigations of flowers up to anthesis may be found on a single inflorescence branch.

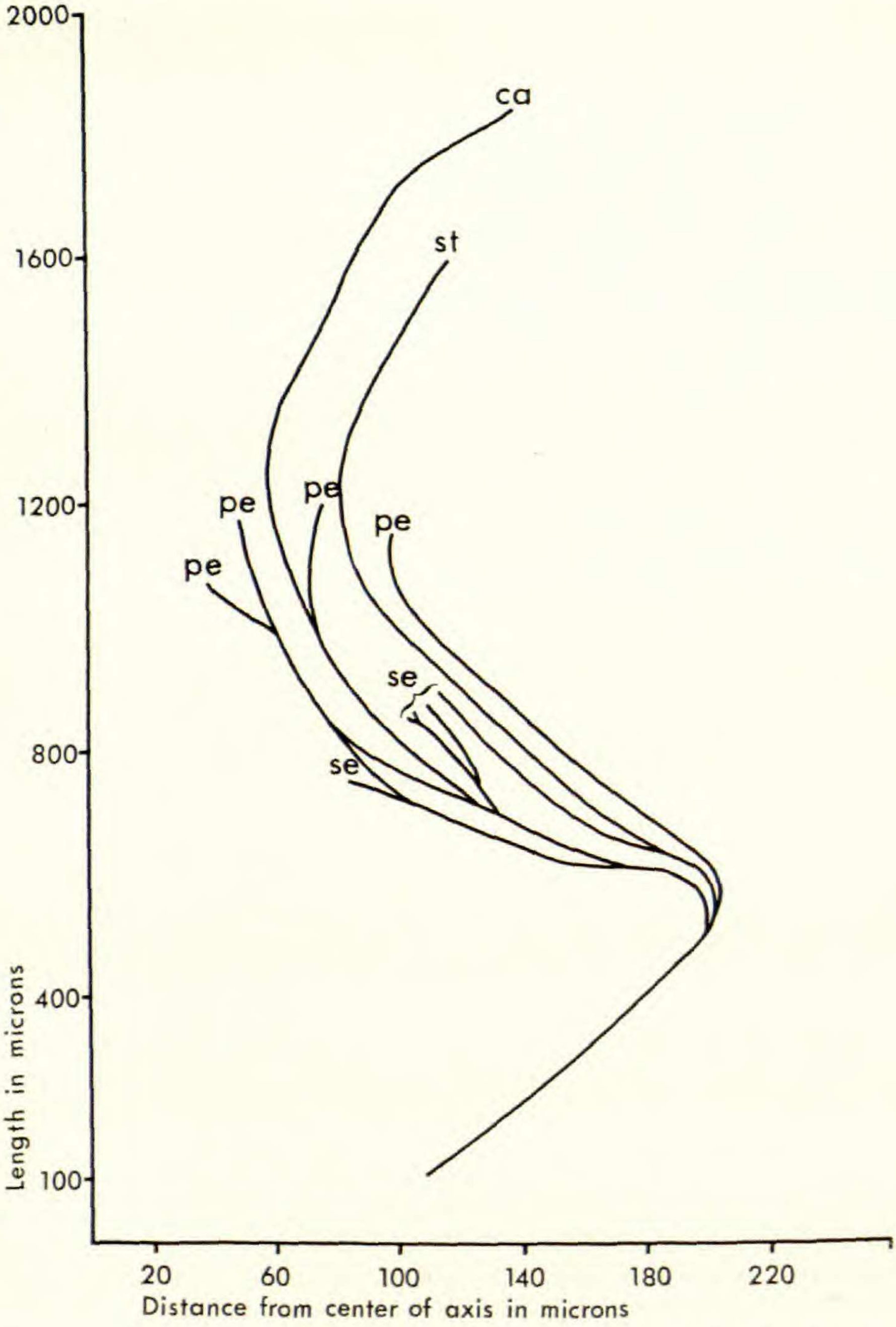


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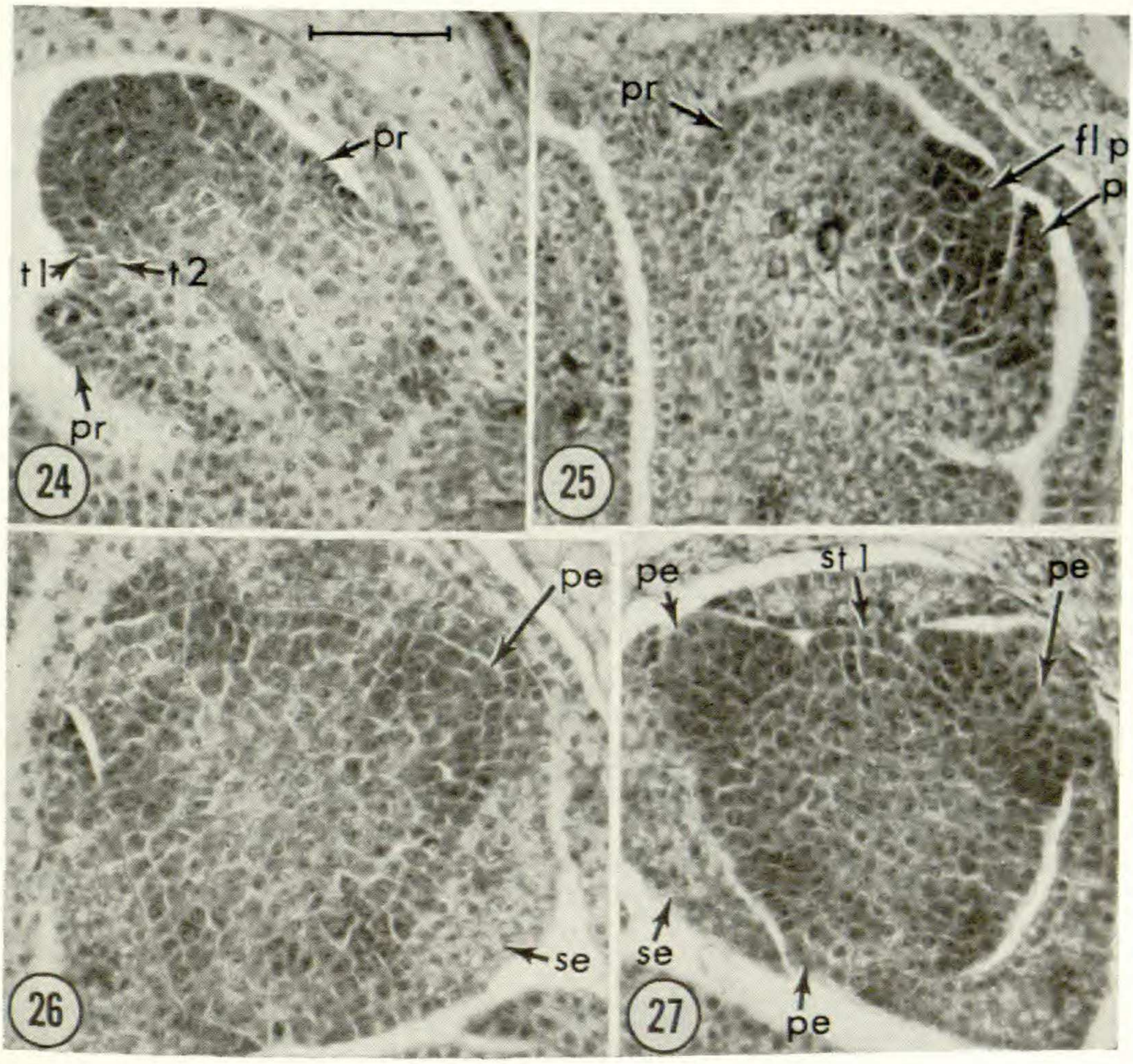
FIG. 23. Plot of the radial path of a major bundle of the floral axis. DETAILS: ca, carpel trace; pe, petal trace; se, sepal trace(s); st, stamen trace.

Above the insertion of the bracteole and subtended floral axis, floral organs arise in acropetal succession on the flanks of the apex. The floral apex is relatively long and is broadly ovate in outline; the one illustrated in FIGURE 24 is ca. 50μ long and 60μ wide. Floral organs are similar in shape in earliest stages and are developed in whorls of three, but each whorl is actually a low spiral since no three organs are at exactly the same level.

Sepals are essentially triangular in outline and slightly narrower than



FIGS. 24–27. HISTOGENESIS. FIG. 24, near-median longisection of a floral apex; FIG. 25, transection showing the primordium of a floral apex and the prophyll (pr) subtending it; FIG. 26, transection of a floral apex showing initiation of petal primordia; FIG. 27, transection of an older floral apex showing young primordia of the lower whorl of stamens. All referable to scale, FIG. 24; scale equals 50μ. DETAILS: fl p, floral primordium; pe, petal; pr, prophyll; se, sepal; st 1, stamen of lower whorl; t 1 and t 2, first and second tunica layers.

other appendages. After initiation, the separate sepal primordia increase in size by apical and marginal growth (FIGS. 26, 27) until the margins of adjacent sepals overlap slightly (FIG. 26). The connate sepal base arises as a unit showing no indication of ontogenetic fusion. Sepals enlarge by subsequent intercalary growth to a length of 3 mm. and envelop all other floral organs until they exceed this length.

Young petal primordia are not initiated until the sepals are approximately 80μ in length. Petal primordia are round to triangular in outline (FIG. 27) and like the sepals develop rapidly at first by apical and marginal meristematic activity. Marginal growth is more extensive in petals than in sepals (FIGS. 28, 31) and in addition an adaxial meristematic region produces thickened tips (FIG. 28). As the flower gradually increases in size (FIG. 5), closed petals protrude farther from the sepals reaching a

length of 5 to 6 mm. in late bud. The thickened apical regions of the petals mature first. Later elongation is by a basal meristematic region (FIG. 37).

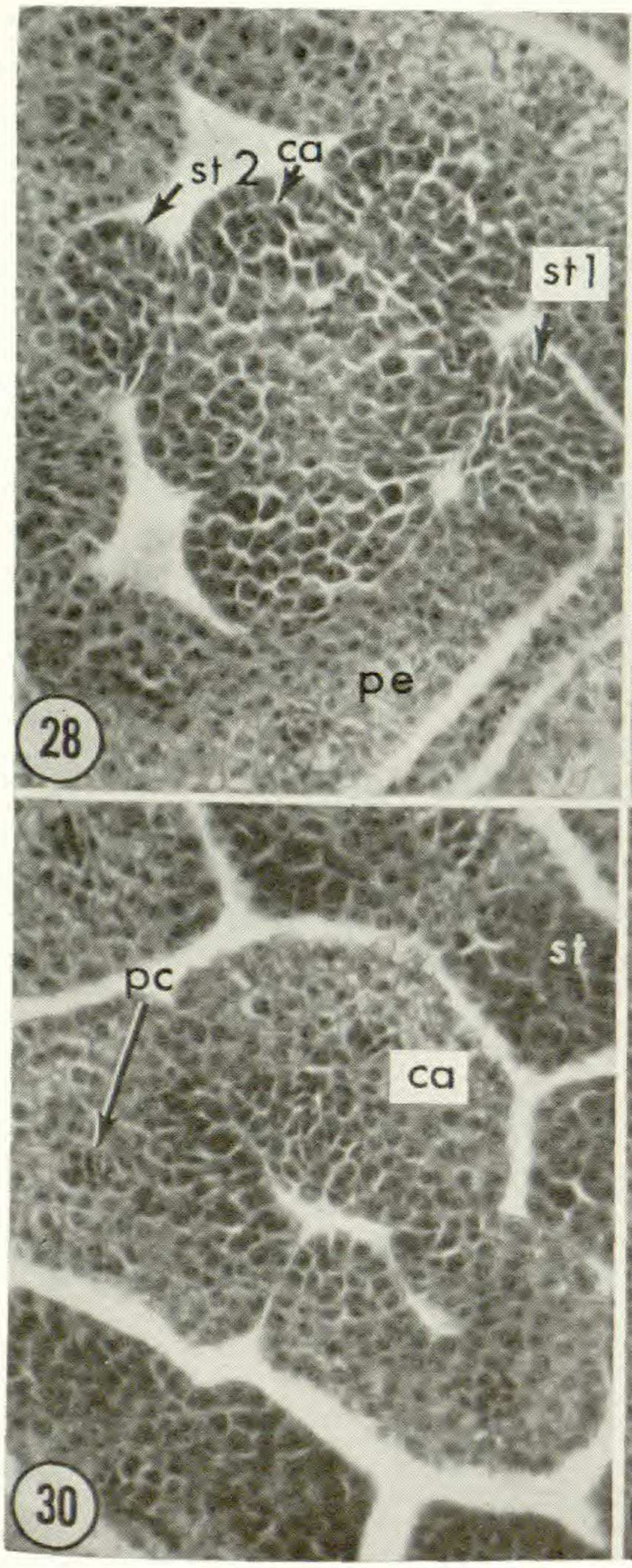
Stamen primordia are initiated in two whorls of three and are elliptic to triangular in outline. FIGURE 27 shows the lower whorl in early stages and FIGURE 28 a later stage of the upper whorl. Initial growth is by apical and marginal meristematic areas. Anther sacs develop in adaxial and lateral positions (FIG. 30). Development of other aspects of the anther is similar to but not as regular as that described by Boke (1949) for *Vinca rosea* (= *Catharanthus roseus*). Sporogenous cells are formed by divisions of primary parietal cells. The tapetum develops later and is one to two cells wide (FIG. 36). In mature stages the endothecium is a single layer of large cells (FIG. 19).

The three carpels are separate in origin (FIGS. 28, 30) and show the familiar crescentic shape illustrated for developing carpels by other authors (Tepfer, 1953; Esau, 1965). In early stages carpels resemble stamens in size and shape (FIGS. 28, 29). Marginal and adaxial growth (FIG. 30) provide the horseshoe-shaped primordium with a solid base and develop what has been called an adaxial lip (Tucker, 1959). The ovule primordium arises ventrally on one side in the base of the shallow cup-like lamina. Directly above the insertion of the ovule, ventral sutures of the carpels are open (FIG. 33). The submarginal position of the ovule can be seen in a young carpel (FIG. 33).

Fusion of the three carpels is ontogenetic and begins in the style. FIGURES 32 to 34 are a series of transections of a gynoecium 230μ in height. Only the upper 130μ of the styles are connate. FIGURE 34 is the first section (proceeding distally) which shows connation. Fusion is by meristematic activity along the appressed ventral faces of the carpels. Initially epidermal cell walls become pointed and interlock (FIG. 35). Subsequent cell divisions produce a solid zone of tissue with no evidence of epidermal layers (FIG. 18). This zone closes the ventral suture of each carpel and joins the three carpels. Fusion progresses gradually toward the base of the gynoecium so that in the flower at anthesis, stylar and ovarian parts are connate but stipes are still separate (FIGS. 17, 18).

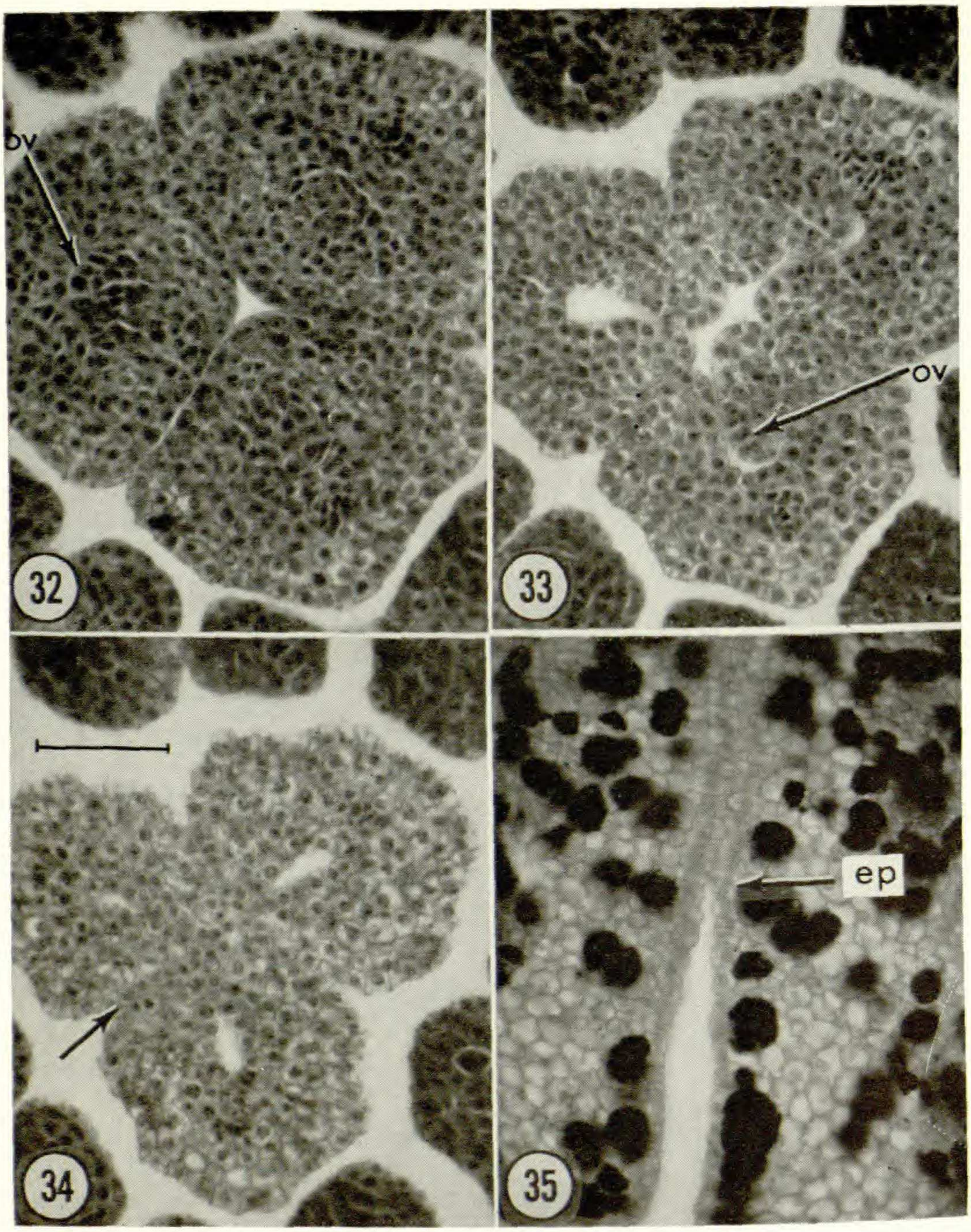
HISTOGENESIS

The floral apex. Esau (1965) states that the amount of zonation of a floral apex may depend on its "determinateness," zonation being lost or obscured in more determinate apices. This applies well to the floral apex of *Nannorrhops* which is relatively indeterminate and shows distinct zonation. The apex (FIG. 24) is zonate with a two-layered tunica, a central group of large corpus initials, and a rib meristem. Barnard (1960) states that two-layered tunicas are relatively common in both floral and vegetative apices of monocotyledons and lists them in the Gramineae, Cyperaceae, Juncaceae, and Liliaceae. Rohweder (1963) has since demonstrated two-layered tunicas in the floral apices of Commelinaceae.



FIGS. 28–31. HISTOGENESIS, continued. FIG. 28, transection of a floral apex showing carpel primordia; FIG. 29, longisection of a young flower, stamen, and carpel primordia approximately equal in length; FIG. 30, transection of a young flower, meristematic activity adaxial in two upper carpels, marginal in lower; FIG. 31, transection of base of an older flower showing adnate carpels, stamens, and petals. All referable to scale FIG. 29; scale equals 50μ. DETAILS: ca, carpel; pc, procambial strand; pe, petal; se, sepal; st, stamen; st 1, stamen of lower whorl; st 2, stamen of upper whorl.

Prophyll and floral primordium. The prophyll is inserted obliquely on the floral axis. The tip adjacent to the subtended floral axis is lower and is initiated first (FIG. 24, right). In early stages it is triangular in outline. There appear to be oblique or periclinal divisions in the dermat-



FIGS. 32–35. DEVELOPMENT OF SYNCARPY. FIGS. 32–34. Successive transections through a young gynoecium ca. 230μ long. FIG. 32, ovarian part of gynoecium, 30μ above base, carpels free; FIG. 33, transection 30μ above FIG. 32, near top of ovules, carpels free, ventral sutures open; FIG. 34, 40μ above FIG. 33, first section showing fusion of carpels; FIG. 35, transection of epidermal layers between two carpels in mature flower to show the pointed and interlocked epidermal cells. All referable to scale FIG. 34; scale equals 50μ. DETAILS: ep, epidermis; ov, ovule; unlabeled arrow, FIG. 34, indicates area of fusion of carpel faces.

ogen in the initiation of the tips of the prophyll. This is the only place where periclinal divisions were observed in the first tunica layer. After initiation, each segment of the prophyll is extended by marginal growth,

the two extensions meeting to complete the abaxial sheathing part of the prophyll. The adaxial part of the sheath is adnate to the axis to a slightly higher level and apparently develops by intercalary growth.

Floral organs. All floral organs are initiated by periclinal divisions in the second tunica and usually only one underlying corpus layer. Initiation of petals is illustrated in FIG. 26, stamens in FIG. 27, and carpels in FIG. 28. Only anticlinal divisions were observed in the first tunica layer during the development of floral organs.

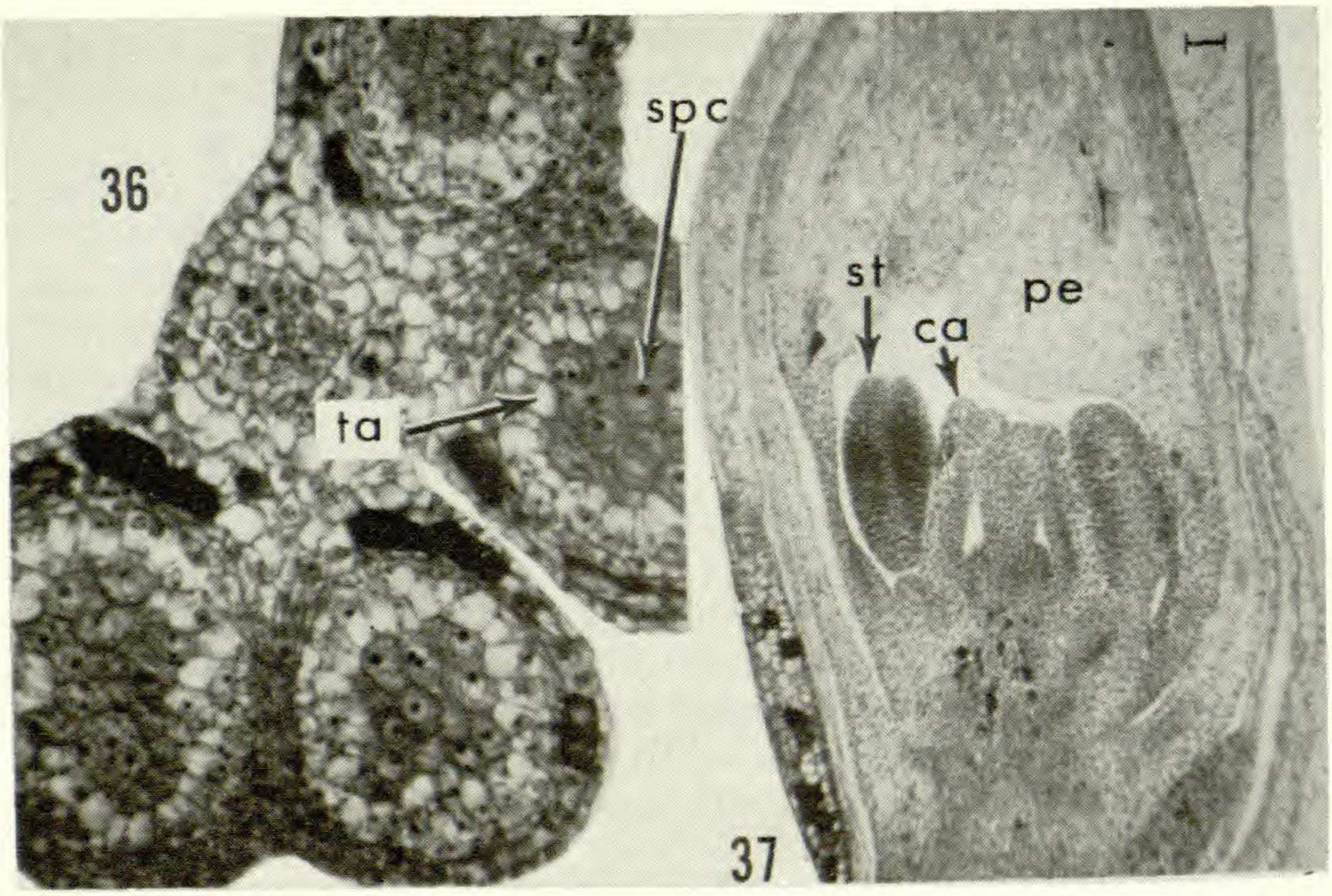
Procambium. The difficulties of determining direction of maturation of procambium are well recognized. In all organs studied for *Nannorrhops*, development of the first procambial strands appears to be acropetal. The first recognizable procambium in a floral stalk is in the form of three central strands. In all floral organs, a single median strand of procambium develops first. This is present in sepals when they are about 160μ high. Stamens and carpels are about 40μ in length when the median strand is recognizable. A single procambial strand is present in petals when they are about 250μ long and three strands are developed when the petals are approximately 330μ in length. The seeming lag in the formation of procambium in the sepals and petals might be accounted for by the rapid early elongation of these organs to enclose developing stamens and carpels which achieve more maturity before elongation.

DISCUSSION

The cincinnus. For obvious reasons the sometimes huge inflorescences of palms have not been readily available for detailed studies. Within the family much diversity is found in both major axes and ultimate flowering units. Evolution in the inflorescence of *Nannorrhops* appears to have resulted in complex patterns of maturation rather than in extreme condensation and/or fusion. Consequently study of this genus is particularly helpful in understanding other genera where more reduction is present. The monopodial systems of major axes are described in a previous paper (Tomlinson & Moore, 1968). With the initiation of the first flower, growth in the inflorescence changes abruptly from monopodial to sympodial.

Designation of the flowering unit in *Nannorrhops* as a cincinnus is not readily evident macroscopically because the five to six flowers within each cluster are successively younger. Details of anatomy and ontogeny, however, show that the basic unit in each flower cluster is a single flower bearing a distinctive bracteole on its axis. In the axil of the bracteole, a new floral primordium is initiated at an angle of approximately 75° on the alternate and abaxial side of each successive floral stalk. Thus the theoretical main axis of the unit is reversed at each primordium and the result is a short scorpioid cyme or cincinnus (Rickett, 1955).

Comparison of the ultimate units of *Nannorrhops* and *Aristeyera* (a



FIGS. 36, 37. FIG. 36, transection of part of anther, for magnification refer to scale FIG. 34; FIG. 37, near-median longisection of young flower; scale equals 50μ. DETAILS: ca, carpel; pe, petal; sp c, sporogenous cells; st, stamen; ta, tapetum.

triad of flowers, Uhl, 1966) suggests that the angle of divergence and position of the bracteole and its subtended primordium determine the shape and consequent definition of the flower cluster. In *Aristeyera*, each floral primordium is borne on the adaxial side of the axis rather than the abaxial as in *Nannorrhops* and the angle of divergence is approximately 25° to 45°. This type of analysis seems to be applicable to many of the diverse ultimate units in palms which are to be treated in detail elsewhere.

Realization that the bract on the flower may be distinctive in shape and anatomy is also useful in interpreting other units. In *Aristeyera* no vascular bundles are present in the bracteole. The second bracteole is bicarinate, however, suggesting a prophyll as in *Nannorrhops*. The significance of the prophyll, a bract which is morphologically and anatomically different from other bracts in the inflorescence, is not apparent at this time.

The flower. Barnard (1955, 1957a,b, 1958) found that in the Gramineae, Cyperaceae, and Juncaceae, stamens were initiated in deeper layers of the floral meristems than other floral organs and, therefore, more closely resembled axial buds. Sharman (1960) also thought stamens (Gramineae) were cauline since they are more like buds in initiation and shape. Other workers (Boke, 1947, 1948, 1949; Tepfer, 1953; Kaussmann, 1963; Kaplan, 1968) have found all floral organs homologous to leaves in patterns of initiation and growth. Because of the nature of palm leaves, developmental patterns are obviously complex and cannot be com-

pared to those of floral organs except in very earliest stages. Leaf primordia in some palms as described by Periasamy (1962) seem similar to those of floral organs in *Nannorrhops* but histogenesis has not been studied.

Evidence from organogeny and histogenesis in *Nannorrhops* suggests that all floral organs are homologous. Stamens and all other floral appendages arise by periclinal divisions in the T_2 and one or more corpus layers. In early stages organs are similar in form and all receive an initial median procambial strand. Later growth patterns differ according to the whorl involved. Sepals develop rapidly and enclose other organs, but remain separate from other floral whorls; while petals, stamens, and carpels become briefly adnate showing zonal growth for a short distance at the base of the flower (FIGS. 14, 31). In addition to evidence from histogenesis, the shape and anatomy of the mature stamens suggest a laminar or foliar nature. The filaments are very wide at the base (FIG. 5). Further the large vascular bundle divides near the base of the filament suggesting the multiple trace condition of foliar stamens (Canright, 1952; Moseley, 1958).

In general the vascular system of the *Nannorrhops* flower is similar to that of *Rhapis* (Uhl, Morrow, & Moore, 1969) and differs from that of the arecoid palms, *Juania*, *Ravenea*, and *Ceroxylon* (Uhl, in press). Major differences are in the vascular supply to the sepals which is much smaller in the latter genera, and in the type of connation and vascular supply of the carpels. In *Juania*, *Ravenea*, and *Ceroxylon*, carpels are connate peripherally and ventral sutures are not completely closed at anthesis; in *Rhapis* carpels are separate and those of *Nannorrhops* are connate by ventral faces. Ventral sutures are closed at anthesis in both the latter taxa. The ovular supply in the arecoid genera is a single bundle formed by fusion of a branch from *each* ventral bundle. In both *Rhapis* and *Nannorrhops*, a branch from *one* ventral and branches of several other bundles form the ovular supply.

Within the palms the *Nannorrhops* flower is relatively unspecialized but within the Coryphoideae, it is one of a few in which extensive syncarpy is developed. Ontogenetic development of syncarpy would seem to relate *Nannorrhops* to other Coryphoideae with separate carpels, and stylar origin of the fusion suggests further connection to a group of coryphoid genera in which the carpels are connate by the stylar regions only. A second type of fusion is seen in the sepals. The connate base arises as a unit with no evidence of union during ontogeny. Many coryphoid genera have connate sepals (Morrow, 1965), the significance of connation here is not understood at the present time.

Much has been written and argued about the basic nature of the angiosperm carpel (Eames, 1961; Tucker, 1959). Consideration of many aspects of carpel structure in palms is beyond the scope of this paper and will be considered in a later survey. It is tempting, however, to point out here that certain features of carpels in the monocotyledons (*Rhapis*, *Nannorrhops*, *Juania*, *Ravenea*, *Ceroxylon*) seem equally and, perhaps,

more primitive than those of the Ranales (*sensu* Eames, 1961). In early stages, carpels of *Nannorrhops* are separate, stipitate, and conduplicate, with open ventral sutures. These are features considered primitive in carpels (Bailey & Swamy, 1951; Baum, 1961). The ovule, in both *Nannorrhops* and *Rhapis*, is attached basally and submarginally to one side of the laminate region. The large vascular supply to the ovule and its origin in both genera, when considered with the unspecialized form, lead to the surmise that a single ovule may possibly be primitive in palms.

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ASPECTS OF MORPHOLOGY OF AMENTOTAXUS FORMOSANA WITH A NOTE ON THE TAXONOMIC POSITION OF THE GENUS

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THE GENUS *Amentotaxus* was established by Pilger in 1916 (Bot. Jahrb. **54**: 41), based on the type species, *A. argotaenia* (Hance) Pilger. This species, described from sterile material only, was originally designated as a member of the genus *Podocarpus*. As soon as its compound staminate strobilus became known, it was transferred to *Cephalotaxus*, and finally to a separate genus, *Amentotaxus*.

The genus *Amentotaxus* is endemic to eastern Asia. It was first collected from a small islet near Hongkong and also from southern Kwangtung. Subsequently it was reported from southern Formosa, western Hupeh and Szechuan, and from southern Yunnan and northern Tonkin (see FIG. 1). Fossil remains have been recorded from Europe and western America (Sporne, 1965). It was generally considered as a monotypic genus; Li (1952), however, recognizes that there are at least four distinct entities (which he considered species) involved, based on color and relative width of the stomatal bands, and geographic distribution. Chuang and Hu (1963), on the other hand, point out that the characters of the stomatal band appear to be less constant, and maintain that there is only one species, namely *A. argotaenia* (Hance) Pilger.

It is rather difficult to make a judgment on this controversial issue without thoroughly examining suitable materials with reproductive structures, which unfortunately, are not available. For simplicity of nomenclature, since all the materials used in this study are from a small locality in southern Formosa, the binomial *Amentotaxus formosana* Li is, accordingly, adopted. It would be interesting to have reports on the strobilate structures based on the materials from other parts of the geographical range of the genus.

The plants of *Amentotaxus* are small to medium-sized, dioecious, evergreen trees. A limited number of them are perhaps in existence, and they grow in almost inaccessible places. Moreover, they are not represented in any botanical garden or arboretum in the world. Owing to the scarcity of material, *Amentotaxus* is among the least known of the gymnosperms. A comprehensive taxonomic description, the only one available, was prepared by Yamamoto (1927); an amendment with a note on leaf anatomy was presented by the same author a few years later (1931). The stomatal and ovulate structures were reported by Florin (1931, 1938–45); his interpretation of the latter, as indicated in a drawing reproduced in 1951, p. 375, *fig. 64*, was apparently based on poorly preserved herbarium material, and is inadequate. Only fragments of the embryonic

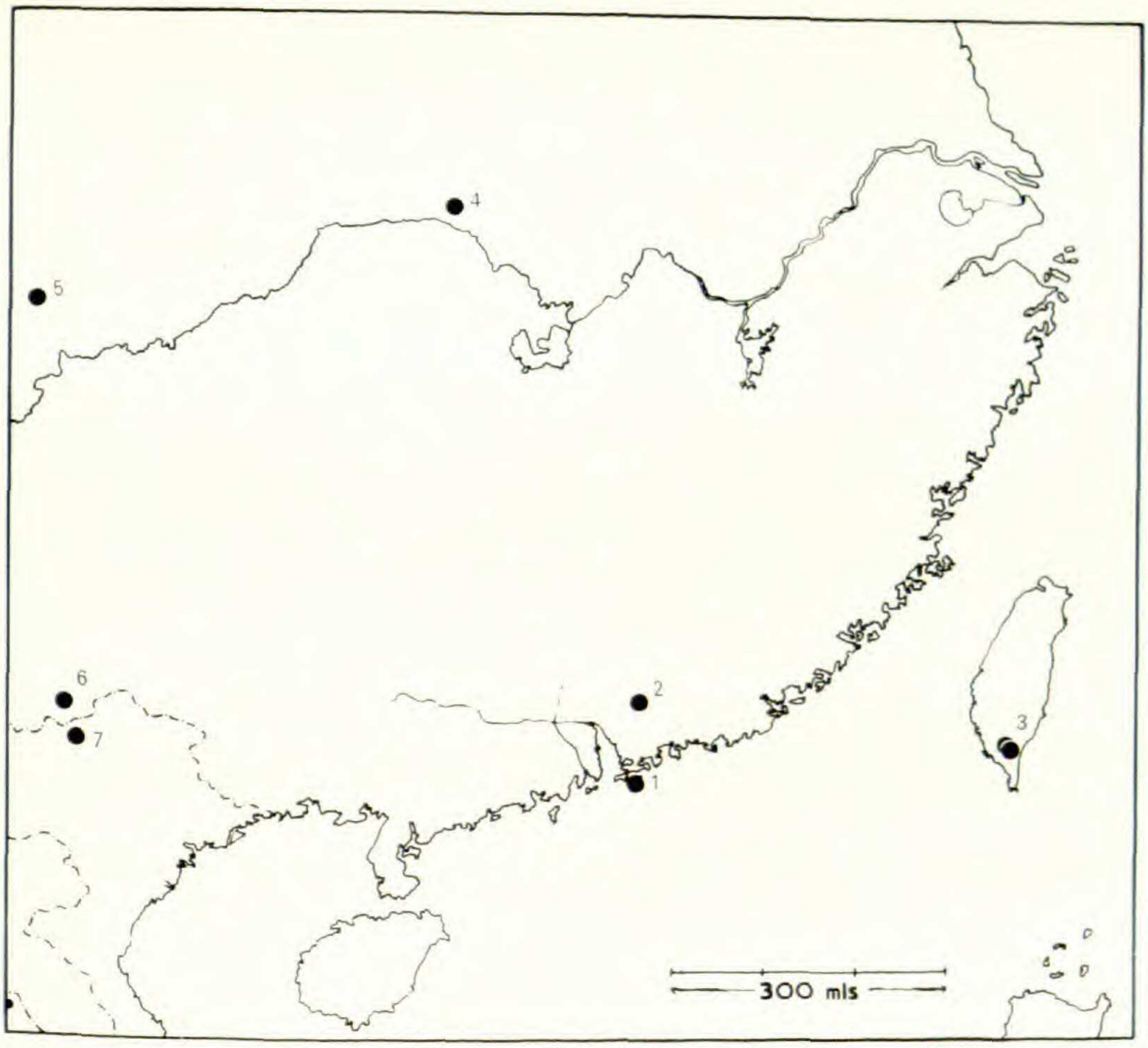

FIGURE 1. Geographic distribution of the genus *Amentotaxus*. 1, Lantao Island, near Hongkong; 2, Mt. Lo-fau-shan, Kwangtung; 3, Taitung and S. Kaohsiung, Taiwan (Formosa); 4, Hsing-shan, Hupeh; 5, Mt. Omei-shan, Szechuan; 6, Makwan, Yunnan; 7, Cha Pa, Tonkin (based on the herbarium specimens cited in Li, 1952).

development were given by Sugihara (1943); and his chromosome number, $n = 11$, on the basis of counts from the female gametophyte, is incorrect, as pointed out by Chuang and Hu (1963). The pollen morphology has been carefully investigated by Erdtman (1957).

MATERIALS AND METHODS

Material preserved in FAA (including leaves, staminate strobili, ovulate strobili, seeds, and seedlings), and dried material (including young ovulate strobili, seeds, and seedlings) taken from herbarium specimens, were received from Professor Ching-en Chang of the Pingtung Agriculture College, Taiwan. All the materials were collected by Professor Chang from near Shin-Huah Farm, Shaw-Jia, Dah-Wu, Taitung, between 1965 and 1968. Clearings of materials were made with 5 percent NaOH at room temperature. Microtome sections 10 to 12 μ thick were stained with a safranin-fast green combination.